E.D. R

Vol. 106. Part 9. Pages 375–392, 12 figs. 15th September, 1955

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LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W. 7

Price 6s. 0d.

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THE WING-VENATION OF THE ORDER PHASMIDA.

By D. R. Ragge, Ph.D., F.R.E.S.
(*British Museum* (*Natural History*))

Manuscript received 3rd August, 1954.
(Read 3rd November, 1954)

With 12 Text-figures.

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1. Introduction.

In a recent book (Ragge, 1955) the author has given an account of the wing-venation of all Orthoptera (*s. lat.*) except the Phasmida. At the time this work was carried out Phasmid nymphs were not available for tracheation studies and no work on the wing-venation of this group was therefore undertaken. Since then, however, an examination of the British Museum (Natural History) Collection has revealed a number of dried specimens whose wing-pads were in a suitable state for making preparations of the tracheae. Also, through the courtesy of Mr. L. C. Bushby of the Zoological Society's Gardens, London, fresh nymphs of *Orxines macklottii* (Haan) have been made available for tracheation studies by the glycerine-jelly method. With the valuable evidence afforded by the nymphal tracheation it has become possible to make a fairly comprehensive study of the wing-venation of these interesting insects, and it is to be

hoped that this will facilitate comparison of the Phasmida with the other Orthopteroid orders and act as a stimulus to taxonomic work within the group.

The only previous published work on Phasmid wing-venation is that of Burt (1932) on the leaf-insect *Pulchriphyllium crurifolium* (Audinet-Serville); the conclusions of this author were based on the nymphal tracheation and agree with those expressed here.

The authors of generic and specific names are given only where these names are first mentioned.

II. Classification.

The classification of the Phasmida has been in confusion for many years. Brunner and Redtenbacher (1906–1908), in their monograph of the group, based some of their subdivisions on unsuitable characters, and there is little doubt that the resulting arrangement is in several cases unsatisfactory. Since the work of these authors there has been no comprehensive study of the group, and since its status has been raised from family to order it has become desirable for its major classification to be completely revised; this, however, will not be possible until the comparative morphology and anatomy of the group have been much more fully investigated.

The system adopted here is largely that of Günther (1953) and is set out below.

Chresmodidae (extinct).
Necrophasmidae (extinct).
Aeroplanidae (extinct).
Aerophasmidae (extinct).
Phylliidae:
- Phylliinae (female hind wings reduced).
- Korinninae.
- Pseudophasminae.
- Aschiphasminae.
- Bacillinae (apterous).
- Heteropteryginae.
- Pygirrhynchinae (apterous).
- Timeminae (apterous).

Phasmidae:
- Pachymorphinae.
- Phasminae.
- Phibalosominae.
- Eurycanthinae.
- Xeroderinae.
- Platycraniinae.
- Podacanthinae.
- Palophinae.
- Necrosciinae.
- Heteronemiinae (apterous).
- Lonchodinae (apterous).

III. Material.

The sixty genera examined are listed below. Where a particular species was used the specific name (when known) is given in the text. Owing, however,

to the taxonomic confusion which at present prevails in the Phasmida, it is often impossible to determine the species name without comparison with the type. Where only the generic name is given in the text, the remarks generally apply to all the alate species of the genus.

PHYLLIIDAE :

Chitoniscus Stål (Phylliinae).
Pulchriphyllium Griffini (Phylliinae).
Phyllium Illiger (Phylliinae).
Neocles Stål (Pseudophasminae).
Prisopus Audinet-Serville (Pseudophasminae).
Dinelytron Gray (Pseudophasminae).
Stratocles Stål (Pseudophasminae).
Olcyphides Griffini (Pseudophasminae).
Pseudophasma Kirby (Pseudophasminae).
Prexaspes Stål (Pseudophasminae).
Isagoras Stål (Pseudophasminae).
Olinta Redtenbacher (Pseudophasminae).
Metriotes Westwood (Pseudophasminae).
Creoxylus Audinet-Serville (Pseudophasminae).
Planudes Stål (Pseudophasminae).
Aschiphasma Westwood (Aschiphasminae).
Presbitus Kirby (Aschiphasminae).
Orthomeria Kirby (Aschiphasminae).
Heteropteryx Gray (Heteropteryginae).
Haaniella Kirby (Heteropteryginae).

PHASMIDAE :

Pharnacia Stål (Phasminae).
Tirachoidea Brunner (Phasminae).
Hermarchus Stål (Phasminae).
Acrophylla Gray (Phasminae).
Ctenomorpha Gray (Phasminae).
Clemacantha Rainbow (Phasminae).
Phasma Lichtenstein (Phasminae).
Eurycnema Audinet-Serville (Phasminae).
Anchiale Stål (Phasminae).
Vetilia Stål (Phasminae).
Onchestus Stål (Phasminae).
Achrioptera Coquerel (Phasminae).
Phibalosoma Gray (Phibalosominae).
Cladoxerus Audinet-Serville (Phibalosominae).
Pterinoxylus Audinet - Serville (Phibalosominae).
Diapherodes Gray (Phibalosominae).
Haplopus Gray (Phibalosominae).
Ophicrania Kaup (Platycraniinae).
Platycrania Gray (Platycraniinae).
Megacrania Kaup (Platycraniinae).
Graeffea Brunner (Platycraniinae).
Podacanthus Gray (Podacanthinae).
Tropidoderus Gray (Podacanthinae).
Extatosoma Gray (Podacanthinae).
Didymuria Kirby (Podacanthinae).
Monandroptera Audinet - Serville (Podacanthinae).
Palophus Westwood (Palophinae).
Ischnopoda Grandidier (Palophinae).
Bactrodema Stål (Palophinae).
Phaenopharos Kirby (Necrosciinae).
Candaules Stål (Necrosciinae).
Orxines Stål (Necrosciinae).
Sosibia Stål (Necrosciinae).
Calvisia Stål (Necrosciinae).
Marmessoidea Brunner (Necrosciinae).
Trigonophasma Kirby (Necrosciinae).
Loxopsis Westwood (Necrosciinae).
Orthonecroscia Kirby (Necrosciinae).
Necroscia Audinet-Serville (Necrosciinae).
Aruanoidea Brunner (Necrosciinae).

IV. TECHNIQUE.

(1) *Preparations of Wing-pad Tracheation.*

For dried nymphs a high refractive index medium (" Naphthrax ", refractive index, when dry, 1·76–1·80) was used. The nymphs were relaxed by immersion in cold water and the wing-pads carefully dissected off. Dehydration and

clearing were then carried out with alcohol and xylol in the usual way. This method is only successful with nymphs which have been collected in the early part of an instar.

Preparations of the wing-pad tracheation of fresh nymphs were made by the glycerine-jelly method (see Ragge, 1955).

(2) *Drawings.*

The drawings of tracheation were made with a camera lucida, and that of the axillary sclerites with a "squared" eyepiece. A photographic enlarger was used for the drawings of adult wings, the latter being placed between two glass squares on the negative stage and the image traced below. This method is a very easy one and produces drawings devoid of distortion.

V. Reasons for the Application of the Homologies Proposed Here.

In order to render the descriptions of venation less cumbersome, the reasons for the application of the names used are given separately in this section. Except where otherwise stated, the arguments put forward apply to the hind wings only; the homologies of the veins of the reduced fore wings may be easily determined from their tracheation and by comparison with the hind wings. For general notes on each of the criteria mentioned here see Ragge (1955, Section IV).

(1) *Fossil evidence.*

Few fossil insects have been classified as Phasmida. The only genera of interest in the present connection are *Chresmoda* Germar (Jurassic), *Necrophasma* Martynov (Jurassic), *Aeroplana* Tillyard (Triassic), and *Aerophasma* Martynov (Jurassic), each forming a separate family. Although regarded as Phasmida by Martynov (1928), these genera have little in common with modern stick-insects (at least to judge by the drawings of Handlirsch (1908), Tillyard (1918), Martynov (1925) and Martynov (1928)), and the relationship should not be looked upon as more than a possibility. With the exception of *Chresmoda* the only parts preserved are the wings, usually in a fragmentary state. The fore wings appear to be fully developed, and extend to the tip of the abdomen in *Chresmoda*. The media is three-branched in this genus, but is bifurcate in *Necrophasma*, four-branched in *Aerophasma*, and seven-branched in *Aeroplana*; in *Chresmoda* there appear to be several branches to the cubitus, and this vein is probably bifurcate in *Aeroplana*. This can only be looked upon as a rather dubious confirmation of what is almost certainly true: that the modern reduced Phasmid fore wing has been derived from a fully developed wing in which the media and cubitus had a greater number of branches.

(2) *Tracheation.*

There are six main tracheal stems in the Phasmid hind wing. By examination of the wing-pad tracheation of nymphs approaching the final moult (when the veins are superimposed on the tracheae) it is easily demonstrated that the costal trachea is not present. Taking the main tracheal stems as representing primary veins, they may therefore be named Sc, R, M, Cu, 1A, and 2A, beginning anteriorly. This conclusion agrees entirely with those arrived at from

other sources with the exception of the sixth tracheal stem, which, for convenience and in the absence of conclusive evidence, is here regarded as being composed of a number of individual units, each with the status of a primary vein (2A, 3A, etc.).

(3) *Form.*

The first two veins of the hind wing are unbranched, thus suggesting that they represent the costa and subcosta. The next two are branched and are followed by two unbranched veins; this does not conflict with the view that these four veins are the radius, media, cubitus and first anal. Reduction in the number of branches to the veins has obscured the usual contrast between an unbranched R_1 and branched R_s. The anal lobe, as in most Orthopteroid insects, is supported by a fan of unbranched veins arising from a common base and named here (largely for convenience) 2A, 3A, etc.

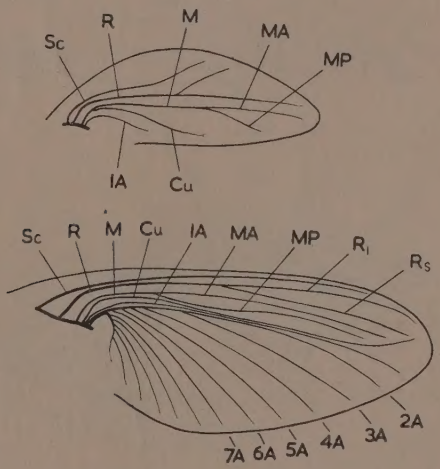


Fig. 1.—The wing-pads of *Phyllium*, male.

(4) *Position.*

If the first six longitudinal veins of a fairly primitive Phasmid (e.g. *Tropidoderus*) are named C, Sc, R, M, Cu, and 1A, respectively, the result is in complete agreement with the conclusions derived from other criteria. In more specialised hind wings the tracheation shows that there is basal fusion between M and Cu and sometimes 1A; when this is taken into account the same argument applies.

(5) *Convexity and Concavity.*

This criterion is not of much use in the Phasmida as most of the corrugation of the wing has been lost. However, the vein named the radius on the basis of other criteria is always convex and, at least basally, Sc and R_s tend to be concave. There is also a tendency for MA and MP to be convex and concave respectively; this supports the view that these branches correspond to those so named by Lameere (1922).

(6) *Basal Articulation.*

The axillary region of Phasmid hind wings is rather modified and, as in the Saltatoria and Dictyoptera, is not of great value in elucidating the homologies of the veins. The base of the radius does, however, articulate with the second axillary, and the media and cubitus are associated basally with a sclerite which may be homologous with one of the median plates found in some of the Acridoid Saltatoria.

(7) *Macrotrichia.*

When macrotrichia are present on Phasmid hind wings they appear to be confined to tracheated veins, thus confirming that these veins are primary.

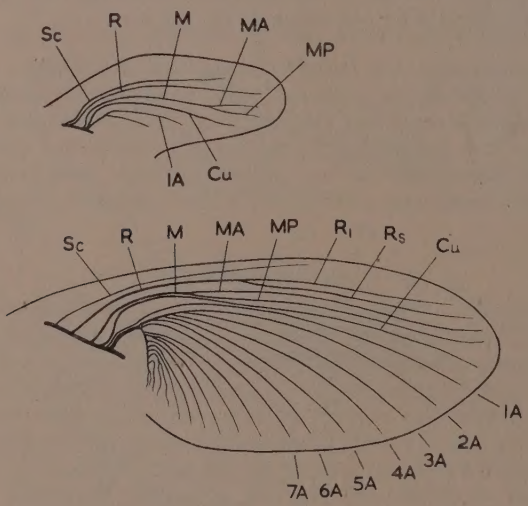


Fig. 2.—The wing-pads of *Metriotes*.

VI. The Tracheation of the Nymphal Wing-pads.

Wing-pad tracheation was examined in *Phyllium* (fig. 1), *Metriotes* (fig. 2), *Hermarchus*, *Tropidoderus childrenii* (Gray) (fig. 3), and *Orxines macklottii*. Tracheae were often visible in the veins of adult wings.

All the longitudinal tracheae arise from a transverse basal trachea. The costal trachea is absent.

(1) *Fore Wing-pad.*

There are probably never more than five longitudinal tracheal stems in Phasmid fore wing-pads, these being respectively Sc, R, M, Cu and 1A. The subcostal trachea is unbranched. This is also true of the radial trachea in most cases, but in the Phylliinae it normally bears at least one anterior branch. In all the fore wing-pads examined the medial trachea was bifurcate. Trachea Cu is normally unbranched but, according to the drawings of Burt (1932, pl. vii),

it is sometimes bifurcate in the female fore wing-pads of *Pulchriphyllium crurifolium*; this trachea is sometimes fused basally with the medial trachea in the Phylliinae. There is one anal trachea in Phasmid fore wing-pads; it is occasionally branched.

(2) *Hind Wing-pad.*

The tracheation of the hind wing-pad is strikingly uniform throughout the order. Trachea Sc is always unbranched; occasionally it is rather poorly developed. The radial trachea is well-developed and normally bifurcate. This is also true of M, though this trachea is sometimes three-branched in the Phasminae (e.g. *Pharnacia serratipes* (Gray); some species of *Tirachoidea* and

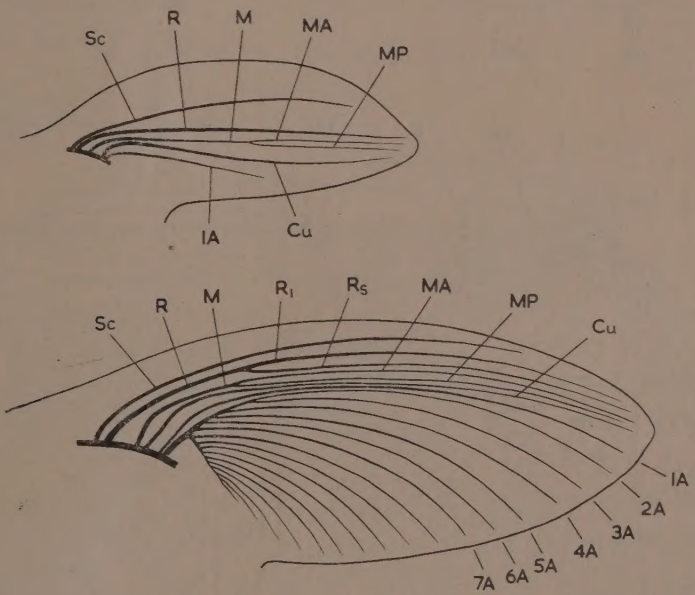


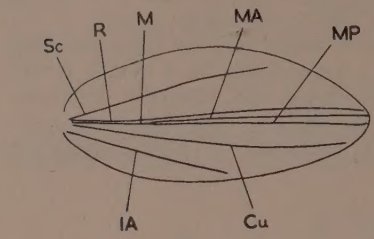
Fig. 3.—The wing-pads of *Tropidoderus childrenii*, female.

Eurycnema), Phibalosominae (e.g. *Diapherodes gigantea* (Gmelin)), and Podacanthinae (e.g. *Podacanthus typhon* Gray). The cubital trachea is always unbranched; it often lies closely against the media trachea (and its posterior branch) in the basal half of the wing-pad. The first anal trachea, as in all other Orthoptera (*s. lat.*), has a base distinct from the remaining anal tracheae; it is always unbranched. The sixth tracheal stem divides into two principal branches: tracheae 2A–7A usually arise from the anterior branch and the remainder from the posterior one. All the anal tracheae are unbranched.

VII. The Venation of the Adult Wings.

The Phylliid subfamilies Bacillinae, Pygirrhynchinae, and Timeminae, and the Phasmid (*s. str.*) subfamilies Heteronemiinae and Lonchodinae, are always

apterous; aptery and brachyptery are common throughout the remainder of the group. Some Aschiphasminae (e.g. *Aschiphasma*) have no fore wings, though the hind wings are fully developed. In some cases the males have normally developed wings while the females are apterous (e.g. *Hermarchus*).



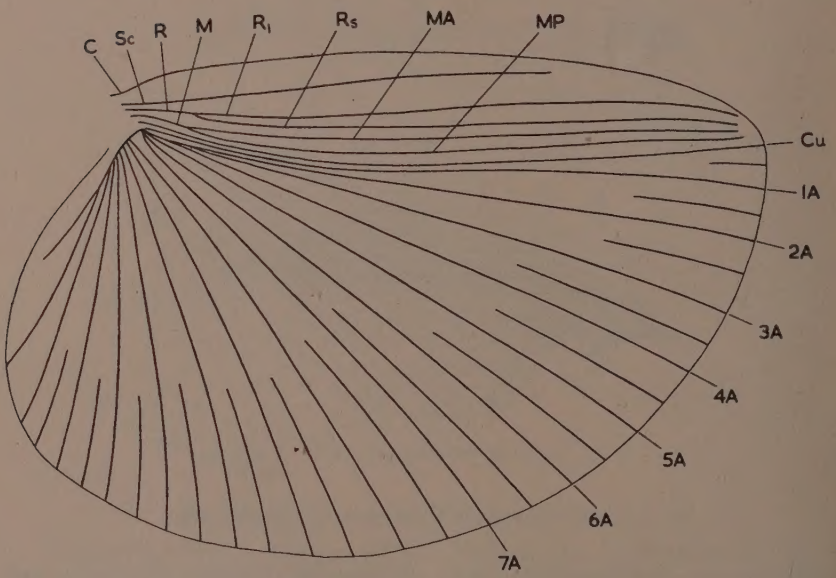


Fig. 4.—The wings of *Tropidoderus childrenii*, female.

(1) *Shape and Areas.*

In most Phasmida the fore wings are reduced to rudimentary flaps, apparently serving the purpose of protecting the axillary region of the hind wings. In the females of some Phasmidae (e.g. *Phasma*; *Megacrania*; *Tropidoderus*, fig. 4), however, the fore wings are almost half the length of the hind wings, and in the Phylliid *Prisopus* they attain three-quarters of their length. In females of the Phylliinae the fore wings cover all or most of the abdomen and the hind wings are vestigial. In brachypterous forms the ratio of the length of the fore wing to that of the hind wing is generally greater,

Where the fore wings are rudimentary they are normally convex and often have a dorsal protuberance in the middle or towards the base ; this is particularly large in some species of *Palophus* and *Ischnopoda*. In the Necrosciinae the fore wings tend to be conical (e.g. *Calvisia*, *Marmessoidea*) ; *Trigonophasma* shows an extreme case of this. Some Aschiphasminae (e.g. *Presbitus*, *Orthomeria*) have vestigial fore wings in the form of bristles. In the Pseudophasminae, Phasminae and Podacanthinae, the fore wings are much better developed and relatively flat. Phasmid fore wings are usually rather tough in texture and cryptically coloured. In females of the Phylliinae the fore wings are shaped and coloured to resemble leaves. There is often a small membranous posterior lobe at the base of the fore wing.

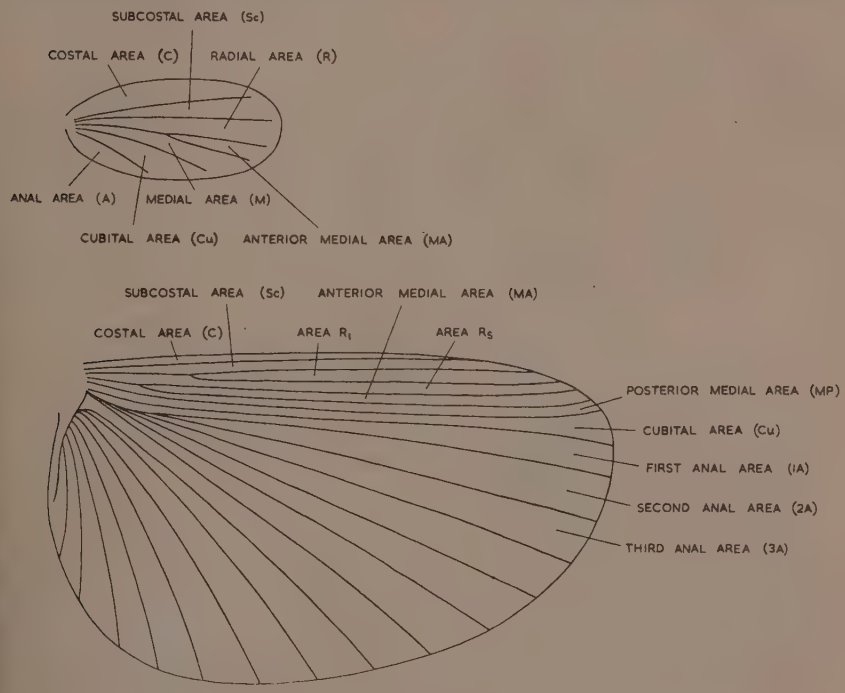


Fig. 5.—The areas of Phasmid wings.

The hind wings of the Phasmida are of the usual Orthopterous shape, being in the form of a foldable fan with the main veins arranged radially. The pre-anal part of the wing is of the same texture as the fore wing, and serves to protect the membranous anal lobe when the wing is flexed.

The areas of Phasmid wings are easily named using the Comstock-Needham System ; a proposed scheme is shown in fig. 5.

(2) *Folding.*

There is sometimes a convex fold at or immediately behind the radius in the fore wing, followed by a concave fold just anterior to the media (e.g. many

Podacanthinae). The expansion of this fold allows the fore wing to fit more closely over the base of the flexed hind wing. When there is a membranous lobe at the base of the fore wing (e.g. many Necrosciinae), it is folded beneath the wing when the latter is flexed.

In the hind wing the first complete fold begins along the anterior edge of the proximal median plate and then continues in the basal part of the first anal area, as shown by the broken line in fig. 6. This fold, which is convex, then crosses 1A into the cubital area and runs to the wing-tip just behind Cu. There is then a concave and convex fold, respectively, in the membrane behind each anal vein. In the pre-anal area a certain amount of concave folding often occurs basally along the line of the cubitus.

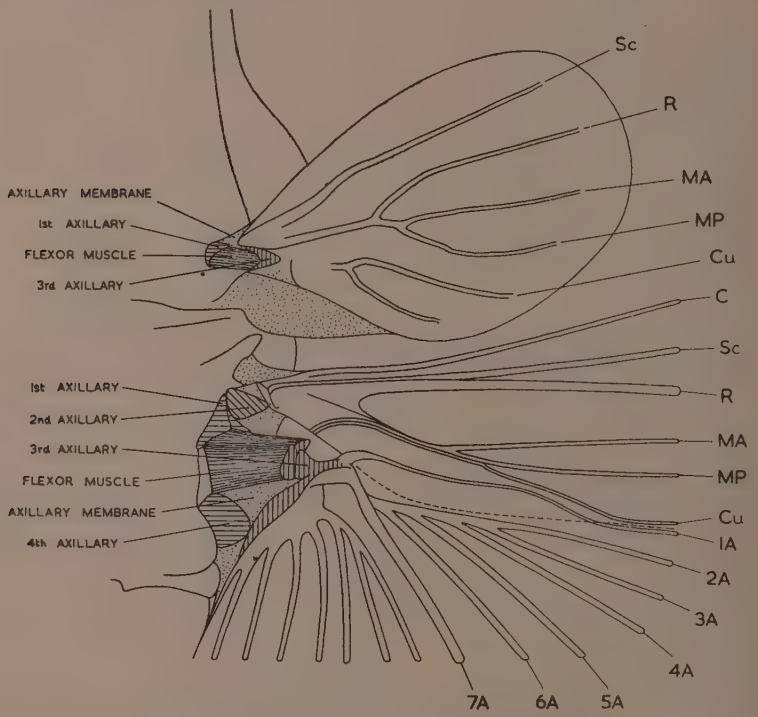


Fig. 6.—The wing-bases of *Orxines macklottii*.

(3) *The Wing-base.*

At the base of each wing there is a flexible region which enables it to be extended or flexed. This consists of an axillary membrane bearing a number of axillary sclerites which intermediate between the veins and the thorax.

No previous work has been published on the basal articulation of Phasmid wings. The following account is based on an examination of fresh specimens of *Orxines macklottii*; the extreme uniformity of Phasmid wing-venation suggests that other species do not differ fundamentally.

(a) *Fore wing.*—The axillary region of the fore wing of *Orxines macklottii* (fig. 6) is much reduced. Only two sclerites are present : a proximal one, which may represent the first axillary, and a distal one —the third axillary—on which is inserted the flexor muscle of the wing.

(b) *Hind wing.*—The fused bases of the subcosta and radius articulate with a well-developed second axillary. This is connected to the metanotum by a movable sclerite which probably represents the first axillary, though it is possible that it is merely a detached portion of the metanotum.

There is a well-developed third axillary attached distally to the fused bases of the anal veins and providing proximally an insertion for the large flexor muscle of the wing. Articulating with the posterior part of the metanotum is a large fourth axillary which probably provides additional support for the base of the anal lobe.

Anterior to the third axillary lies a sclerite hinged to the fused bases of the media and cubitus. It is probable that this represents the proximal median plate found in the Acridoidea, as its antero-lateral border forms a prominent convex fold when the wing is flexed. The distal median plate, if present, would in this case be incorporated in the fused bases of M and Cu.

There appear to be no tegulae or humeral plates in the wing-bases of *Orxines macklottii*.

(4) *The veins.*

The veins of Phasmid wings may be classified as follows:

(a) Ambient veins.
(b) Longitudinal veins:
  (i) Primary veins.
  (ii) Secondary veins.
(c) Cross-veins.
(d) Archedictyon.

These terms are used in the sense defined by Ragge (1955, p. 38 *et seq.*).

(a) *Ambient veins.*

Well-developed ambient veins are not normally found in Phasmid wings. The margin of the fore wing, however, is often thickened slightly, and the thickening is sometimes definite enough to be looked upon as a vein. This is particularly true of the Phylliinae, in which the males often have a fairly clear ambient vein along the anterior margin of the fore wing.

Ambient veins are not found in Phasmid hind wings.

(b) *Longitudinal veins.*

(i) *Primary veins :*

The costa (*C*).—There is no costa in Phasmid fore wings. In the hind wing this vein supports the anterior margin, but is usually very poorly developed. Males of the Phylliinae, however, have a fairly well-developed costa in the hind wing. The costa is always unbranched and, when well-developed, is convex.

The subcosta (*Sc*).—This is the first definitive vein in the fore wing, where it lies some distance behind the anterior margin.

In the hind wing the subcosta runs parallel to, and just behind, the costa.

It rarely reaches the extremity of the wing and is often rather poorly developed : in *Metriotes* (fig. 7), for example, it is less than half the length of the wing.

The subcosta is always unbranched ; it tends to be concave in both pairs of wings, and is sometimes quite markedly so (e.g. *Phyllium*, male).

The radius (*R*).—The radius is the most strongly developed vein in the fore wing and in the pre-anal part of the hind wing. In the fore wing it usually has a roughly central position and is associated with the tubercle, when this is present ; it is usually a single stem but normally has at least one anterior branch in the Phylliinae (see figs. 8 and 9).

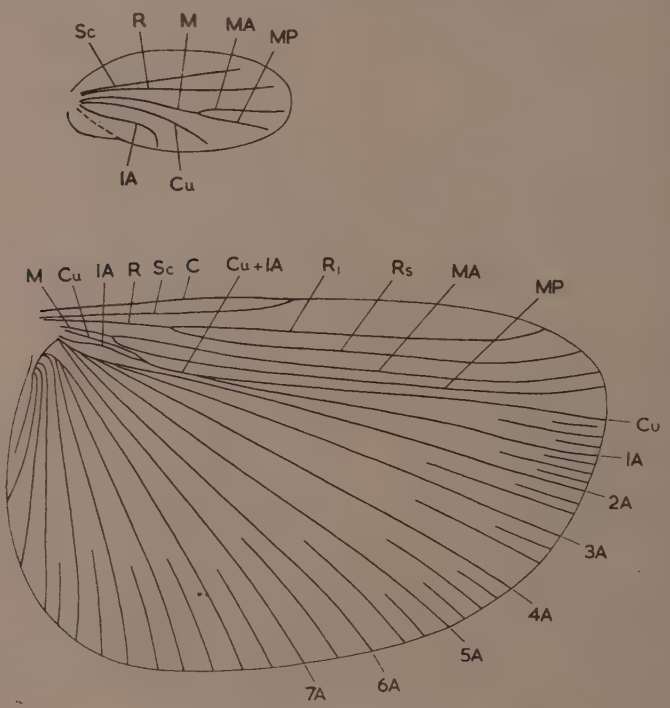


Fig. 7.—The wings of *Metriotes*.

In the hind wing this vein lies just posterior to the subcosta. It is usually divided into two unbranched veins, R_1 and R_s, which run parallel to each other to the wing-tip ; among the exceptions to this are *Necroscia*, *Aschiphasma*, and the males of *Marmessoidea*, in which R is unbranched in the hind wing. In a few species either R_1 or R_s is occasionally bifurcate (e.g. some species of *Hermarchus*). The bifurcation of R is usually at the base of the wing. It becomes progressively more distal, however, in *Haplopus*, *Marmessoidea* and *Chitoniscus*, for example, and in some species of *Pulchriphyllium* is in the distal half of the wing.

The main stem of the radius is always convex in both pairs of wings ; in the

hind wing this is usually also true of R_1, and R_s, when present, tends to be concave.

The media (*M*).—The media is usually the only branched vein in the fore wing, being simply bifurcate as a rule. Where the fore wings are very reduced this vein is often fused basally to the radius (e.g. *Orxines*).

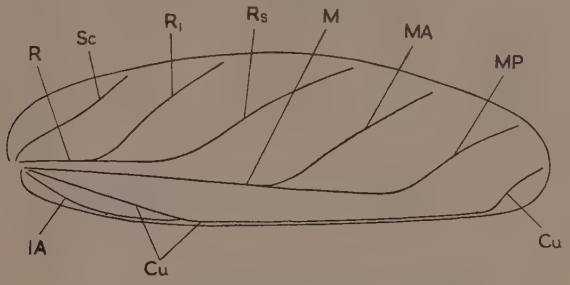
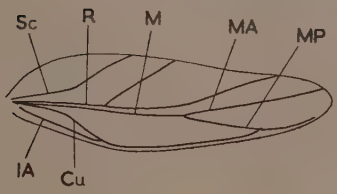


FIG. 8.—The female fore wing of *Phyllium*.



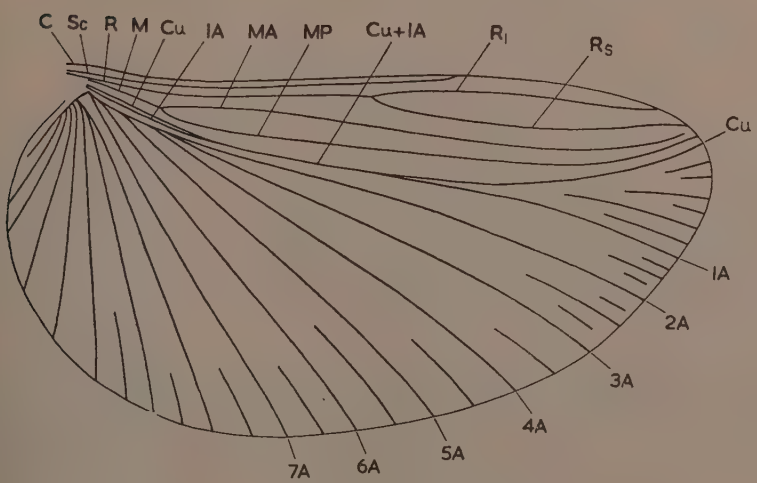


FIG. 9.—The wings of *Phyllium*, male.

In the hind wing this vein is similar in form to the radius, giving rise characteristically to two equally developed branches (MA and MP) near the base of the wing. Unlike the radius, however, the bifurcation of the media is always

basal, the main stem never occupying more than a sixth of the wing-length. Occasionally the media is three-branched (e.g. males of *Pharnacia serratipes* (fig. 10) and of some species of *Tirachoidea*; males of *Diapherodes gigantea* (fig. 11); females of *Podacanthus typhon*: females of some species of *Eurycnema*). The third branch (MP_2) usually fuses immediately to Cu for most or all of its length, but there is only slight basal fusion in *Pharnacia serratipes*, for example, and in the holotype of *Eurycnema magnifica* Kirby MP_2 and Cu are quite free throughout their length.

The media and its branches show no definite convexity or concavity, but in some hind wings MA and MP show a slight tendency to be respectively convex and concave.

The cubitus (*Cu*).—Unlike other Orthopteroid insects the Phasmida normally have an unbranched cubitus in both pairs of wings. A bifurcate cubitus was found in one or two of the hind wings examined, but these were probably freak

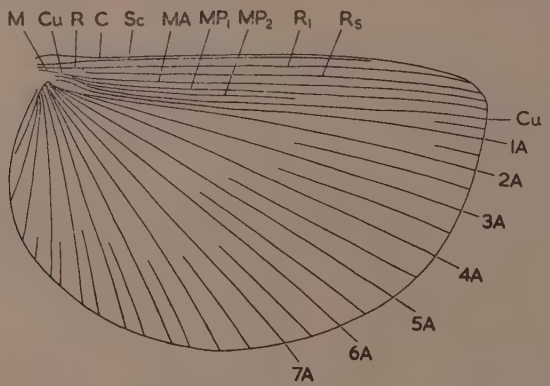


FIG. 10.—The hind wing of *Pharnacia serratipes*, male.

instances not typical of the species. In the hind wing Cu is commonly fused to M and MP (e.g. *Calvisia maculicollis* (Westwood), fig. 12), MP alone (e.g. *Cladoxerus ditomus* (Westwood)), MP_2 alone (e.g. *Pharnacia serratipes*), M, MP, and then 1A (e.g. some species of *Candaules*), or 1A alone (e.g. *Phyllium*), for part of its length. In more primitive hind wings (e.g. *Tropidoderus*, and some species of *Eurycnema*) Cu is quite free from M and 1A.

The cubitus shows no definite convexity or concavity in the fore wing, but in the hind wing is usually concave towards the base.

The anals (1A, 2A, etc.). Except where the fore wings are rudimentary, they have one anal vein (1A) which is sometimes fused basally to Cu.

In the hind wings the anal veins are arranged in the usual Orthopteroid fashion, providing support for the large anal fan. The first anal is rather distinct from the remainder, though articulating basally with the same axillary sclerite (the third). Unlike other Orthoptera, the Phasmida do not possess a very strongly developed 1A, the second to seventh anal veins (particularly the latter) usually being appreciably stronger. This group of anal veins is very characteristic of Phasmid wings; the six veins (2A–7A) of which it is invariably

composed arise posteriorly from one basal stem, while the remaining anal veins arise anteriorly from another. This corresponds with a similar division in the nymphal tracheae. These two groups of anal veins may correspond to 2A and 3A in other non-Orthopteroid insects, but there is insufficient evidence for this to be regarded as more than a possibility. The number of anal veins in the second group is variable, but is usually between eight and fourteen.

(ii) *Secondary veins.*

There are normally no accessory veins in Phasmid wings. Intercalary veins are not found in the fore wing or in the pre-anal part of the hind wing, but there are usually several in the anal lobe, alternating with the primary anal veins.

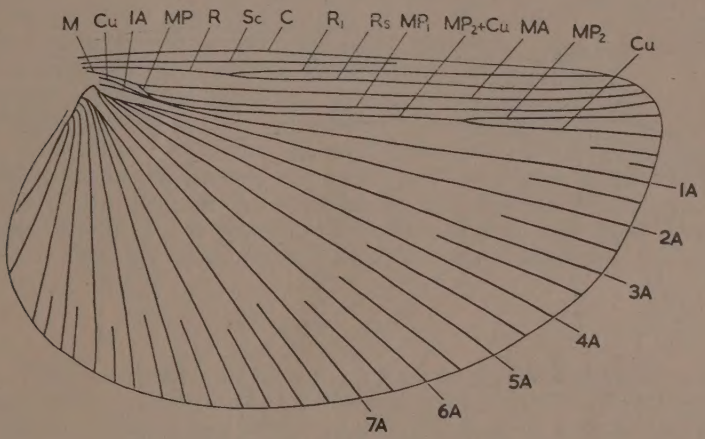


FIG. 11.—The hind wing of *Diapherodes gigantea*, male.

(c) *Cross-veins.*

There are no cross-veins in the fore wings. In the hind wings, however, they are found throughout the anal lobe and often in the more posterior part of the pre-anal region of the wing, sometimes extending up to the subcosta (e.g. *Calvisia*) or even the costa (e.g. the Phylliinae).

(d) *Archedictyon.*

The spaces between the veins of the fore wing are supported by archedictyon. In the hind wing the more anterior part of the pre-anal region is covered with archedictyon, but it rarely extends behind the cubitus.

VIII. CONCLUSIONS.

The most striking feature of Phasmid wing-venation is its uniformity. Even the hind wings of the Phylliinae, a group very much modified in other morphological features, are almost identical in venation to those of the more typical members of the order. This uniformity is, of course, accentuated in the nymphal

tracheation, as can be seen by comparing figs. 1, 2, and 3. The following venational features are common to all alate Phasmida :

(1) The costa, subcosta, cubitus and anal veins are unbranched.

(2) The radial sector is almost always present and always unbranched.

(3) The media is divided basally into two or three branches.

(4) The first anal vein is less strongly developed than the second to seventh anal veins.

(5) The second to seventh anal veins form a group distinct from the remaining anal veins.

(6) There are no accessory veins.

(7) Intercalary veins are confined to the anal lobe.

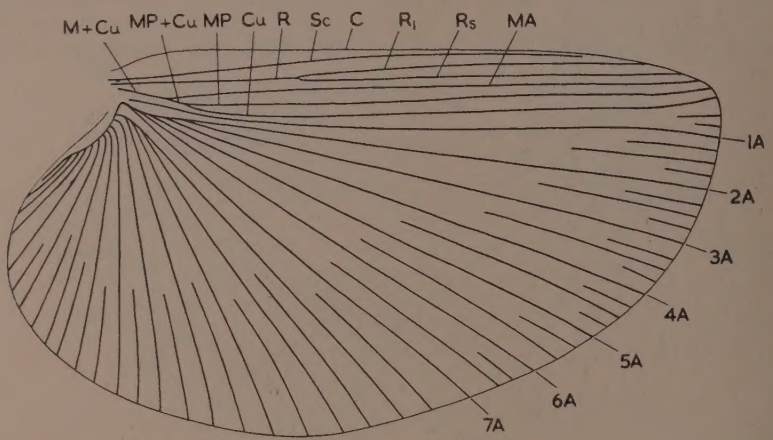


Fig. 12.—The hind wing of *Calvisia maculicollis*, female.

The lack of branching on the part of most of the veins results in a reduced venation, and the wings of the Phasmida are most clearly characterised by negative features, such as the unbranched cubitus and radial sector, and lack of accessory veins. One positive diagnostic character, however, is provided by the association of the second to seventh anal veins.

The variable amount of fusion, especially near the wing-base, between M, Cu, and 1A, provides characters of great systematic importance which have hitherto been largely ignored. Most differences of this sort are chiefly useful at generic and specific level ; the unbranched radius occurs in isolated genera (or even species) in two subfamilies (Aschiphasminae and Necrosciinae) and the third medial branch (MP_2) in similar circumstances in three subfamilies (Phasminae, Phibalosominae and Podacanthinae). It is very probable that the three-branched media is a primitive feature ; in all cases where it has been found the cubitus has been free from the media at its base, though usually fusing with MP_2 for a short distance. In *Eurycnema magnifica* (holotype, female), however, MP_2 and Cu are free from fusion throughout their length ; this species (and several other species of *Eurycnema*) also has a three-branched media in the female fore wing, though here it is MA which is bifurcate. The fore and hind

wings of *Eurycnema* can therefore be looked upon as having the most primitive type of venation in the Phasmida, and *Aschiphasma*, in which R and M are unbranched and the fore wings absent, may be regarded as the opposite extreme. The bifurcation of the radius is basal in the more primitive Phasmid wings, becoming progressively more distal as specialisation increases. The wings of *Tropidoderus* (fig. 4), *Pharnacia* (fig. 10), *Metriotes* (fig. 7) and *Diapherodes* (fig. 11) show successive stages in the distal movement of this bifurcation, and also show a gradual increase in the degree of fusion between M and Cu. . The fore wings are generally larger where the hind wings have a more primitive venation and very reduced fore wings are usually associated with a more specialised venation in the hind wing.

The wing-venation of the Phasmida suggests no close relationship between this group and the other Orthopteroid orders. The anal fan is, of course, also present in the hind wings of the Dictyoptera, Saltatoria, Plecoptera and Isoptera (*Mastotermes* Froggatt), but the distinct group formed by veins 2A–7A in the Phasmida is not found elsewhere. A simply bifurcate media of the Phasmid type is found in the Acridoid and Grylloid Saltatoria and in the Plecoptera, but these are probably cases of convergence by reduction. The unbranched cubitus is unique among the Orthopteroid orders, and the absence of accessory veins provides sharp contrast to the Saltatoria and Blattoid Dictyoptera. The Grylloid Saltatoria and Mantoid Dictyoptera are the only other groups of insects in which the radius typically shows a simple bifurcation.

IX. Summary.

1. There has been no previous attempt to survey the wing-venation of the Phasmida or to apply the Comstock-Needham terminology throughout the group. The author's intention has been to remedy this situation and thus to furnish useful material for phylogenetic and taxonomic studies both within the group and among the Orthopteroid orders as a whole.

2. Sixty genera were examined. These included representatives of almost all the winged subfamilies.

3. The criteria used in elucidating the homologies of the veins were those of tracheation, form, position, convexity and concavity, basal articulation, and macrotrichia.

4. From a consideration of these criteria names based on the Comstock-Needham System are given to the veins and areas of Phasmid wings.

5. Although the wing-venation of the group is remarkably uniform, it is suggested that there are several features of taxonomic importance which have hitherto been largely ignored. There are no grounds, on the basis of wing-venation, for regarding the Phasmida as being closely related to any of the other Orthopteroid orders.

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